ACOUSTIC BEHAVIOR OF TROPISTERNUS ELLIPTICUS, T. COLUMBIANUS, AND T. LATERALIS LIMBALIS IN WESTERN OREGON (COLEOPTERA: HYDROPHILIDAE)

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Abstract

Besides the known stridulation in stress, calling, and courtship functional categories, acoustical signals in 2 new categories, male copulation and female aggression (male rejection), are described for the genus *Tropisternus*. Two male positions are recognized during courtship: the forward position and the probing position. *T. columbianus* restricts stridulation to the probing position, whereas the other 2 species stridulate in both positions. All species of *Tropisternus* studied emit stress and calling chirps. *T. ellipticus* also has either male buzzes or slow trills during both probing and copulation. *T. columbianus* has male courtship slow trills. *T. lateralis limbalis* has male ticking during calling, and it has courtship fast trills identical to the subspecies *T. l. nimbatus*. Females of *T. ellipticus* and *T. columbianus* have a similar aggressive signal, the rejection buzz, which terminates courtship by males. Although courtship sounds were emitted during calling, calling sounds were never emitted during courtship.

INTRODUCTION

Tropisternus ellipticus, T. columbianus, and T. lateralis limbalis commonly occur in quiet aquatic habitats of western Oregon. Three functional categories of acoustic signals (Alexander, 1967, 1968) have been described for Tropisternus: disturbance (stress) by both sexes, calling by both sexes, and male courtship (Ryker, 1972, 1975b). I here describe acoustic signals in the same categories for these western Oregon species and report 2 new functional categories: male copulation and female aggression (male rejection). Also, 2 male positions are recognized during courtship. The stridulatory apparatus for Tropisternus was described previously (Ryker, 1972).

MATERIALS AND METHODS

Sounds were recorded with an Uher 4000L portable tape recorder at a tape speed of 19 cm/sec (7.5 ips), using a rubber coated clip-on contact microphone completely immersed in the water (Kellogg 1960). Playback for analysis utilized the same recorder, which had a measured frequency response of 0.05-10 kHz +/-3 db, and a Kay Sona-Graph 6061A, 0.085-8 kHz spectrum analyzer, using the Wide Band Filter for precision in timing measurements. Recording and behavioral observations were carried out in a 8.5 X 16.5 X 6 cm (depth) plexiglas chamber. To dampen sound reflection, the floor and one side wall were covered with 2 layers of asbestos screening oriented at 45° to each other; and the chamber was screen-partitioned into 3 chambers, with one of the end chambers filled with aquatic plants.

Observations were made in the opposite end. The microphone was in the narrow central chamber. Bright incandescent illumination was provided during observations, and the water temperature was held between 22-27°C to allow normal behavior and eliminate temperature effects on sound parameters (Ryker 1976). Student's t-test for unequal sample sizes was used for statistical evaluations of signal parameters.

RESULTS

Courtship Positions

Males of Tropisternus used visual cues at close range (1-2 cm) to orient to females (Ryker 1976) and usually mounted the backs of the females immediately upon contact. The male began a rather stereotyped courtship dance while mounted (Young 1958), including stridulation (Ryker 1972) in one or both of 2 courtship positions. The male first oriented head to head, and then moved anteriorly and leaned down over the head of the mounted beetle to touch palpi with it. While in this position, the "forward" courtship position, the male encircled one of her palpi with both of his palpi, which curved slightly backward (Fig. 1a). Then he shifted across to the other side of her head, his palpi dragging across hers until they encircled her second palpus (palpus-touching). Palpus-touching was repeated as the male rhythmically shifted from one side of the female's head to the other. As the male moved from one side to the other, his body pivoted so that his hind leg opposite to the side he was on was free to sweep across the surface of her elytra (hindleg sweeping) (Fig. 1a). The male swept 2 to 4 times per side in all species studied. While positioned forward, some species of Tropisternus stridulated some or all of the time; others were silent.

After shifting from side to side at the head several times, the male stepped backwards and probed the female's genital area with his extended aedeagus (probing). Most species studied stridulated in the probing position, but some were sometimes silent. Males mounted in the probing position rhythmically tapped either 1 or both foretarsi on the female's elytra (Fig. 1b). The rate of tapping was different for different species. In *T. columbianus*, for example, males tapped about 4 times per second.

Copulation occurred only if the female permitted it by lowering her abdomen to receive him. Females sometimes began a violent side to side shaking motion, often accompanied by stridulation, as males mounted them. Females also frequently struck at the male's palpi with their forelegs as the males attempted palpus-touching. I interpret female shaking and stridulating as rejection behavior, as it usually terminated courtship.

Tropisternus ellipticus (LeConte)

T. ellipticus occurs throughout the western United States, Mexico, and Central America (Spangler, 1960). In western Oregon this species breeds in temporary pools in the spring and river rock pools in the summer, and overwinters in ponds and lakes (Ryker 1975a).

The stridulations of T. ellipticus were separated into 10 types according to sex and behavioral context: 4 male and 2 female chirps, 3 types of male buzzes, and 1 female buzz. Data from measurements of the sounds, includ-

ing means, standard errors, sample size, and statistical significance, are summarized in Table 1.

Calling chirps of males, when alone or when responding to the sight or acoustical signals of other beetles, and of responding females were similar in duration (P<0.05). However, the male stress chirp was of longer duration (P<0.05), and the female stress chirp was even longer (P<0.01) (Table 1) (Fig. 2a, b).

Buzzes (slow stridulations in which the component pulses are distinguishable but too rapid to be counted by ear) may be produced by males when alone, when responding to the sight or stridulations of other beetles, during courtship in the forward position, during probing, and during copulation (Fig. 2c, e). However, males may be silent in each of those contexts. The durations of male buzzes were essentially similar in all contexts (P < 0.05)(Table 1). Pulse rates of buzzes of males alone, responding, or in the forward courtship position were similar (P < 0.05), and these contexts are combined as "courtship buzz" in Table 1. Male buzzes emitted during probing and copulation are similar in duration to other buzzes, and have

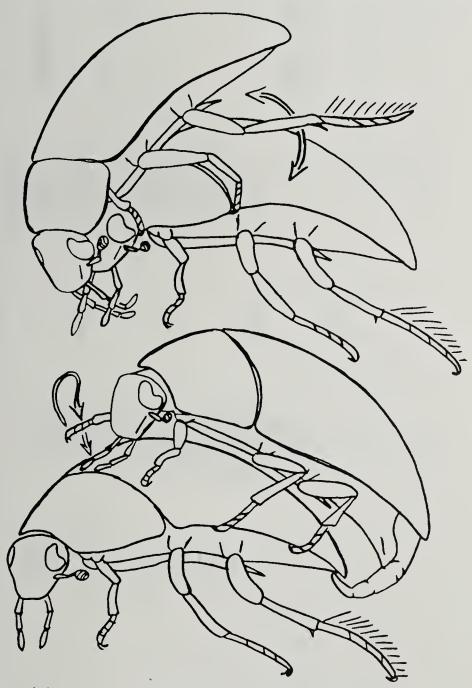


Fig. 1. Courtship positions of *Tropisternus*: a) forward position with palpus-touching and hindleg-sweeping; b) probing position with foreleg-tapping.

FORWARD

a

b

PROBING POSITION pulse rates similar to each other but slightly faster than other buzzes (P < 0.05).

Females of *T. ellipticus* sometimes produced buzzes accompanied by rocking or shaking from side to side during courting by males (*rejection buzz*) (Fig. 2f). These were of longer duration and faster pulse rate than male buzzes (P < 0.05).

Probing and copulation were occasionally also accompanied by rhythmic chirps (*slow trills*) by the males (Fig. 2d). Slow trills during probing were shorter in duration and slower in chirp rate than slow trills during copulation (P < 0.05).

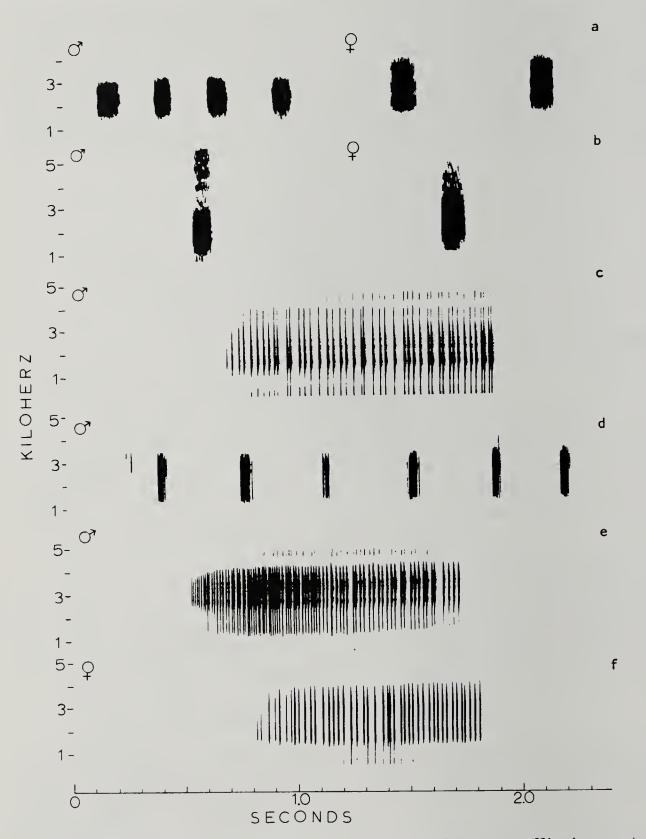


Fig. 2. Sonagraphs of stridulations of *Tropisternus ellipticus*: a) stress chirps (27°, 28°C); b) calling chirps (28°, 27°C); c) buzz, forward position (28°C); d) rhythmic probing chirps (24°C); e) copulation buzz (29°C); f) rejection buzz (28°C).

Tropisternus columbianus Brown

T. columbianus occurs from the west coast of the United States, British Columbia, Canada, and Baja California, Mexico, eastward to the edge of the Great Plains in Michigan (Spangler 1960). In western Oregon this species is found in permanent ponds and lake edges throughout the year.

Table 1. Summary of sound data for <u>Tropisternus ellipticus</u>.

Sound	Duration (seconds)				Pulse rate (pulses/second)				
	x	SE	n	Stat. signif.	x	SE	n	Stat. signif.	
f calling chirp	0.075	0.005	(18)	al					
calling chirp	0.072	0.003	(27)	a					
stress chirp	0.088	0.004	(74)	ь					
stress chirp	0.098	0.004	(74)	с					
rejection buzz	1.070	0.073	(20)	d	42.5	1.74	(20)	h	
f courtship buzz	0.830	0.032	(89)	е	50.0	2.70	(89)	i	
f probing buzz	0.889	0.099	(13)	е	60.7	6.63	(13)	j	
' copulation buzz	0.868	0.132	(5)	e	59.0	3.63	(5)	j	
					Chirp rate (chirps/second)			ond)	
f probing slow trills	0.065	0.006	(50)	f	2.5	0.20	(10)	k	
d copulation slow trills	0.092	0.006	(46)	g	1.95	0.11	(11)	1	

Table 2. Summary of sound data for <u>Tropisternus</u> columbianus.

Sound	Duration (seconds)				Chirp rate (chirps/second)				
	x	SE	n	Stat. signif.	x	SE	n	Stat. signif.	
♂ calling chirp	0.060	0.002	(60)	a^{l}					
<pre>♀ calling chirp</pre>	0.081	0.003	(25)	Ъ					
d stress chirp	0.113	0.003	(42)	с					
9 stress chirp	0.130	0.003	(61)	d					
d probing trill	0.123	0.004	(46)	е	2.12	0.093	(46)	£	
d copulation trill	0.141	0.010	(14)	е	1.71	0.092	(14)	g	
d unmounted trill	0.127	(one of only)							
					Pulse rate (pulses/second)				
? rejection buzz	0.688	0.043	(31)		43.1	4.8	(19)		

Table 3. Summary of sound data for <u>Tropisternus lateralis limbalis</u>.

Sound		Duration (seconds)				Chirp rate (chirps/second)				
	x	SE	n	Stat. signif.	x	SE	n	Stat. signif.		
f calling chirp (alone)	0.082	0.004	(22)	a^{l}						
f calling chirp (response)	0.155	0.025	(8)	ь						
calling chirp (response)	0.172	0.034	(17)	Ъ						
f stress chirp	0.106	0.003	(73)	с						
stress chirp	0.102	0.003	(71)	с						
f unmounted trill	0.022	0.002	(23)	d	7.8	0.2	(23)	е		
f courtship trill	0.024	0.001	(63)	d	8.5	0.2	(63)	f		
f copulation trill	0.023	0.002	(14)	d	8.4	0.4	(8)	f		
f chirp-trill	0.020	0.006	(23)	d	8.1	0.1	(23)	g		
ず chirp-walk				`	3.4	0.1	(6)	~		
					Tick rate (ticks/second)					
ticking	0.803	0.038	(39)		10.8	0.6	(39)			

¹ different letters in same vertical column indicate significant differences at P < 0.05 level.

The stridulations of T. columbianus were separated into 10 types according to sex and behavioral context: 3 types of chirp for each sex, 3 types of male trills, and 1 female buzz. Of these, I have no recordings of males or females alone; however, other studies indicate that both sexes chirp when alone (Ryker 1976). Data from measurements of these sounds are summarized in Table 2.

When alone or when responding to acoustic or visual stimuli, both sexes emitted *calling chirps* that were of shorter duration than the *stress chirps* (Fig. 3a, b). Both the calling chirp and the stress chirp of females were longer than the corresponding chirps in males; i.e., there were 4 distinct chirps (P < 0.05).



Fig. 3. Sonagraphs of stridulations of *Tropisternus columbianus*: a) stress chirps (26°, 25°C); b) calling chirps (29°, 22°C); c) probing trill (23°C); d) copulation trill (27°C); e) rejection buzz (28°C).

Males trilled or were silent when responding to acoustic or visual stimuli, always trilled during courtship when probing, and rarely during copulation (Fig. 3c, d). Durations of *probing* and *copulation trills* were similar, but the rhythm, or chirp rate, of the probing trill was faster than that of the copulation trill (P < 0.05). The trill of an unmounted male was even faster than these 2; but because only 1 beetle was represented in the data, the rate could not be compared statistically.

Females of T. columbianus sometimes emitted a rejection buzz similar in pulse structure to that of T. ellipticus females as they shook and rocked from side to side during male courtship (Fig. 3e). This was the only buzz produced by this species.

Tropisternus lateralis limbalis (LeConte)

This is a montane race of T. *lateralis* that occurs west of Colorado, from British Columbia southward into Central Mexico (Spangler 1960). In western Oregon, this species overwinters in ponds and breeds in temporary pools or pond edges with a soft mud bottom.

The stridulations of T. *l. limbalis* were separated into 13 types according to sex and behavioral context: 3 types of chirps for each sex, 5 male trills, the male chirp-walk, and male ticking. Data from measurements of these sounds are summarized in Table 3.

When alone or when responding to acoustic or visual stimuli, both sexes emitted *calling chirps* (Fig. 4b). The male chirp given when alone was of shorter duration than the other chirps (P < 0.05); I have no recordings of solitary females. Sampled response chirps of both sexes were also few in number; however, the ones recorded were longer in duration than male calling chirps when alone. Male *stress chirps* were similar in duration to female stress chirps and longer than male chirps when alone (P < 0.01) (Fig. 4a).

Males trilled at times when alone, when approaching to mount another beetle, when mounted at the head, when probing, and sometimes when copulating (Fig. 4c, d). The durations of chirps making up trills were similar for all trills. However, the chirp rate of unmounted trills was slightly faster (P < 0.05) than the others. Chirp rates of *courtship trills* in both the forward and probing positions are similar to the chirp rate of *copulation trills* (P < 0.05).

Males produced *ticking* sounds at times when alone, particularly after being stimulated by chirping or by visual contact with another beetle (Fig. 4e). Usually the immediate response to such stimulation was to chirp, but in less than a minute a male would switch to ticking if he was not further stimulated. Ticking phrases contained about 8 ticks, ranging between 5 and 13 ticks.

After contacting another beetle, a sexually responsive male often began walking stiff-legged and jerkily and produced a series of small sounds I have termed the *chirp-walk* (not illustrated). Chirp-walking males invariably attempted to mount any beetle-like object coming into visual range. Chirp-walk sounds may be a by-product of the state of excitement of the male as he searches for a female, with no signal value.

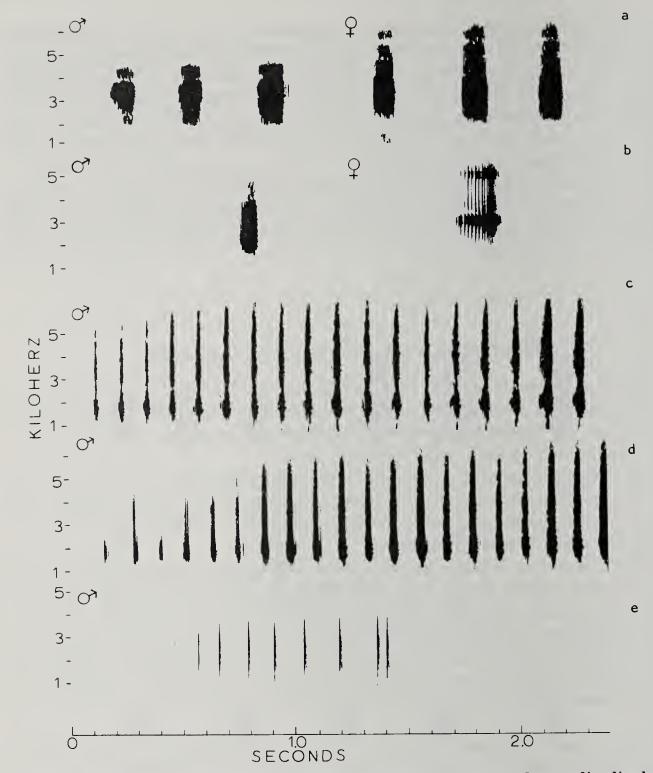


Fig. 4. Sonagraphs of stridulations of *Tropisternus lateralis limbalis*: a) stress chirps (27°C); b) calling chirps (27°, 21°C); c) courtship trill (23°C); d) copulation trill (22°C); e) ticking (23°C).

DISCUSSION

A distinction between the forward and the probing positions during courtship is necessary because a male of *Tropisternus* may restrict stridulation to 1 of the 2 positions. For example, *T. columbianus* generally restricts its slow trill to probing, remaining silent in the forward position. In contrast, *T. ellipticus* stridulates more frequently in the forward position than during probing (Ryker 1976). Statistical comparisons of signal parameters permit a listing of the number of physically distinct stridulations for each species, although the living beetles may not discriminate between all of these. Six distinct signals are produced by T. ellipticus: calling chirps, stress chirps, male buzzes, probing slow trills, copulation slow trills, and the female rejection buzz. Seven distinct signals are produced by T. columbianus: male calling chirps, female calling chirps, male stress chirps, female stress chirps, male courtship trills, and the female rejection buzz. Four distinct signals are produced by T. lateralis limbalis: calling chirps, stress chirps, male trills, and male ticking.

The calling chirps of the 3 western Oregon species of *Tropisternus* are quite similar in duration. Although the chirp of *T. columbianus* is statistically shorter, the other 2 are not different. The leading edge of the calling chirp of *T. l. limbalis*, however, has a distinctive pulse structure not found in the other 2 species.

In courtship behavior, T. ellipticus is the only species of the 3 to have a buzz, and the fast trill of T. *l. limbalis* is distinguishable from the slow trill of T. columbianus. Males of T. ellipticus sometimes give a similar slow trill during probing, but the duration of each component chirp is only half as long as that of T. columbianus.

Ticking sounds of T. *l. limbalis* and "courtship" buzzes of T. *ellipticus* produced in calling situations do not provide signal specificity between these 3 species because the mating sequence frequently begins with mounting by the male upon contact with a female, with no prior signals. Therefore, signals during courtship probably have a more important role in species recognition than have calling signals.

Males of *Tropisternus* may produce several sounds in calling situations, but the calling chirp is never used during courtship. Also, males usually have a single courtship sound (except *T. ellipticus*), but courtship sounds may also be produced during calling and copulation.

Aggressive behavior by females towards courting males has been observed many times in all species studied. Females of T. mixtus (Ryker 1972), T. lateralis nimbatus (Ryker 1976), T. ellipticus, and T. columbianus have a characteristic buzz that accompanies other rejection behavior like shaking and striking the male's palpi with forelegs. These buzzes are variable in duration and have similar pulse rates in these 4 species.

Surprisingly; the signaling repertoire of T. *l. limbalis* in Oregon is identical to that of T. *l. nimbatus* in Michigan even in measurements of chirp durations and trill rates, although the Oregon subspecies includes more ticks in each ticking phrase. The slow trills of courting males of T. *columbianus* are distinctive from those of other species. The courtship buzz of T. *ellipticus* is similar to those known in T. *glaber* and T. *natator*, although slower in pulse rate. Signals of sympatric species in Oregon are distinctive, as one would expect. However, the added importance that the present study has led me to place on species recognition during courtship (rather than during calling) brings up the question how females of T. *natator* and T. *glaber* in Michigan, which have extremely similar mounted courtship buzzes (Ryker 1972), select males of their own species. Tactile or chemical signals may play a more important role in this genus than has yet been demonstrated.

ACKNOWLEDGEMENTS

A Grant-in-Aid of Research from Sigma Xi, The Scientific Research Society of North America, helped to defray travel costs to study sites. I thank J. A. Rudinsky and D. M. Burgett, Oregon State University, for helpful criticism of the manuscript. This study was part of Ph.D. dissertation research by the author at Oregon State University.

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